

Preliminary cladistic analysis of the bivalve family Cardiidae

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Abstract. Phylogenetic relationships within the bivalve family Cardiidae have been examined by cladistic analysis. Thirty-six of the approximately 180 cardioid supraspecific taxa are analyzed, including members of each of the generally recognized cardiid subfamilies, plus the cardioid families Lahilliidae, Lymnocardiidae, and Tridacnidae. Data for each taxon have been taken from a single species. For the outgroup, a hypothetical ancestor has been constructed from data for the carditids *Cyclocardia ventricosa* (Gould) and *Cardita variegata* Bruguière. The data consist of 54 characters and 170 character states. Results indicate that the families Lahilliidae, Lymnocardiidae, and Tridacnidae should be given subfamilial status within the Cardiidae. *Septocardia* is removed from the Cardiinae and placed in its own subfamily, and the subfamily Protocardiinae is found to be paraphyletic. The Laevicardiinae, as proposed by Keen (1936, 1951, 1969, 1980), is shown to be polyphyletic: *Cerastoderma* is a lymnocardiine; *Dinocardium* is a cardiine; *Clinocardium* is the type genus of the Clinocardiinae. In addition to *Laevicardium*, only *Habecardium* and *Fulvia* remain in Laevicardiinae. The Trachycardiinae is found to be a monophyletic taxon within the Cardiinae. The subfamilies Clinocardiinae, Tridacninae, Lymnocardiinae, and Fraginae form a monophyletic clade. *Sawkinsia*, long considered a tridacnid, belongs with the Cardiinae.

Bivalves of the family Cardiidae, or cockles, display a wide spectrum of shell shapes, ribbing and ornamentation patterns, hinge morphologies, and numerous other conchological features. Their complex morphology, accompanied by their good fossil record, allows the cardiids to be evaluated evolutionarily, ecologically, functionally, and phylogenetically in considerable detail.

The higher-level taxonomy of the Cardiidae has been more thoroughly studied than that of most other groups of bivalves (Dall, 1901; Stewart, 1930; Keen, 1936, 1937, 1951, 1969a, 1980; Fischer-Piette, 1977; Kafanov and Popov, 1977; Popov, 1977; Wilson and Stevenson, 1977; Voskuil and Onverwagt, 1989). Kafanov and Popov (1977) made the only detailed attempt to reconstruct the phylogenetic history of the group.

Traditionally, the superfamily Cardioidea comprises: (1) the Cardiidae; (2) the extinct, southern hemisphere Lahilliidae; (3) the brackish-water Lymnocardiidae, confined to eastern Europe and southwestern Asia; (4) the Tridacnidae, or giant clams [Keen (1969b), Kafanov and Popov (1977), and Scarlato and Starobogatov (1979) have placed the giant clams in a separate superfamily]. Kafanov and Popov (1977) contended that the Lahilliidae belonged to the Arcticoidea. However, as noted by Finlay and Marwick (1937) and Marwick (1944), the hinge of *Lahillia* is of the cardiid, not arcticoid type; the lack of external ornament is apparently a case of convergence. This classification has not been taken for granted, and representatives of the Tridacnidae, Lahilliidae, and Lymnocardiidae are included in this analysis.

Additionally, *Cardium acuticostatum* d'Orbigny, 1842, is included. Wilckens (1904) placed the Cretaceous *C.*

acuticostatum in *Cardium* (*Bucardium*), which Keen (1980) indicates is known from only the Miocene to Recent.

Boss (1971), Kafanov and Popov (1977), Keen (1980) and Ponder *et al.* (1981) placed the enigmatic *Hemidonax* in the Cardioidea. However, Scarlato and Starobogatov (1979) argued that *Hemidonax* is aligned with the Donacidae. After examination and comparison of the shell and of the anatomy (both external and internal) of *Hemidonax* to both cardiids and donacids, I cannot justify placing *Hemidonax* as a member of the Cardioidea. However, neither can I place *Hemidonax* within the Donacidae. Instead, I favor placing *Hemidonax* as *incertae cedis* within the order Veneroidea, until a phylogenetic analysis of the Veneroidea is undertaken.

Virtually all cardiid taxonomy is based on hard parts, with the exception of Starobogatov's (In: Kafanov and Popov, 1977) study of stomach structure. Most of what is known about the anatomy of cardiids comes from the study of the common cockle, *Cerastoderma edule* (Linnaeus) (see Ménégau, 1890; Johnstone, 1899; Zugmayer, 1904; Küpfer, 1915; Roche, 1925; Atkins, 1937; Graham, 1949), which is taken as a model for the entire family. Furthermore, Russian malacologists (Kafanov and Popov, 1977; Popov, 1977; Taktakishvili, 1987) place *Cerastoderma* within the subfamily Lymnocardiinae - which, less *Cerastoderma*, Keen (1969a, 1980) considered to be a separate family within the superfamily Cardioidea. The only treatment of comparative anatomy of the cardiids is that of Pelseneer (1911).

The goals of this study are to: (1) determine the status and content of subfamilies erected by previous workers; (2) propose a preliminary phylogenetic hypothesis for the family.

Characters and character states are briefly described herein and will be treated fully in future publications.

MATERIALS AND METHODS

There are about 180 generally accepted cardioid genera and subgenera (see Keen, 1969a, 1980; Kafanov and Popov, 1977; Vokes, 1980; Taktakishvili, 1987). It is not feasible currently to run a computer-driven cladistic program for such a large number of taxa. The 36 taxa chosen in this study include at least one representative of each of the cardiid subfamilies accepted by Keen (1969a, 1980), Kafanov and Popov (1977), and Voskuil and Onverwagt (1989). As stated above, the tridacnids (*Tridacna*), lahilliids (*Lahillia*), and lymnocardiids (*Hypanis*) are also represented in this analysis (the suffix -ids is used in a vernacular sense until their taxonomic placement is discussed thoroughly). Kafanov and Popov's (1977) and Keen's (1980) classification scheme for the taxa analyzed in the present study is given in appendices 1 and 2.

A cladistic analysis of the 36 taxa with 54 characters comprising 170 character states (appendices 3 and 4) was made using PAUP 3.0d (Swofford, 1989). The accelerated transformation option (ACCTRAN) was used, and steps were not added to terminal taxa with polymorphisms. Synapomorphies for each node are presented in appendix 5.

Character states were encoded from a single species of each genus or subgenus. Most of the taxa are represented by their type species. Exceptions are those taxa for which

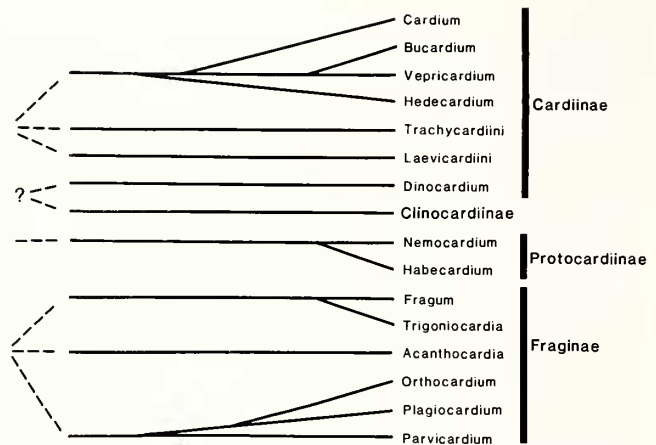


Fig. 2. Evolutionary scenario for the Cardiidae from Kafanov and Popov (1977). Only those taxa included in both the present study and Kafanov and Popov (1977) are shown.

(1) material of the type species was unavailable, or (2) anatomical material was not available for the type (e.g. *Nemocardium*, for which the type species is extinct), but was available for another species generally assigned to that taxon. Taxa represented by species other than the type are listed in appendix 6. Therefore, this analysis should be taken as a phylogeny for these species only. Character states presented may not be constant throughout all species of a given genus. Because there is considerable disagreement over what constitutes a genus or a subgenus in the Cardiidae, all terminal taxa will be considered to have equal rank as genera; no distinction will be made between genera and subgenera, except as noted in the text.

Citations in the character list (appendix 3) refer to previous discussions of that character. Except for the information on *Cyclocardia* (see below), character 12, and character 8 for *Parvicardium* (from Pelseneer, 1911), all character states were encoded from examination of specimens.

The Cardiidae are generally accepted as having been derived from a member of the Carditoidea [Cox, 1949; Keen, 1969a, 1980; Newton, 1986; but see Morris (1978) and Morris *et al.* (1991)]. These authors have postulated an evolutionary scenario of *Palaeocardita* originating from some primitive carditid or permophorid, with *Septocardia* then originating from *Palaeocardita*. *Palaeocardita* is usually placed with the Carditidae (Chavan, 1969). However, examination of the one species of *Palaeocardita* available to me, *Palaeocardita silberlingi* Newton *et al.*, has led me to place this species within the ingroup Cardiidae, on the basis of its cardinal teeth, which are arranged as in *Septocardia* and *Protocardia* [see Newton *et al.* (1987) for a discussion of this species]. Therefore, to represent the outgroup, a hypothetical ancestor was constructed with information from the Recent carditids *Cardita variegata* Bruguière and *Cyclocardia ventricosa*

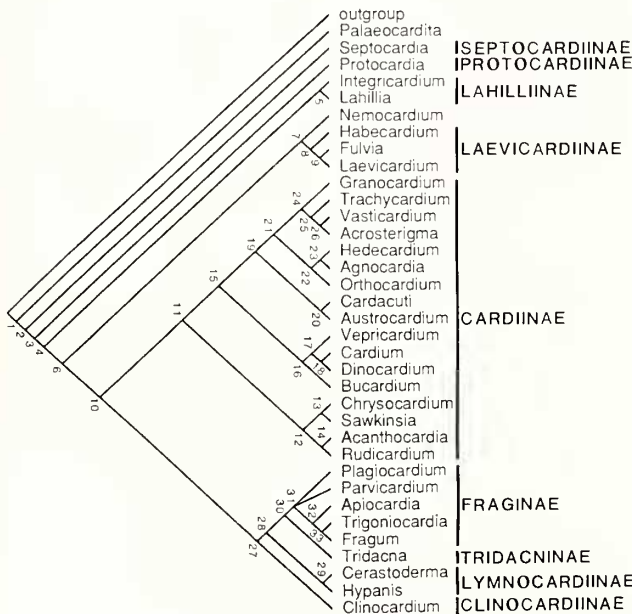


Fig. 1. Majority-rule consensus tree of 50 most parsimonious trees. Nodes 21 and 22 supported by 60% of trees; nodes 28 and 30 supported by 70% of trees; node 31 supported by 90% of trees; all other nodes supported by 100% of trees. Synapomorphies supporting each node given in appendix 5.

(Gould). Character states for *C. ventricosa* were taken from information in Yonge (1969). For characters 6 and 30, the two carditids provided conflicting information, and hence the states are scored as missing ("?").

Most characters are unordered. It was possible to construct character state trees based on ontogeny for characters 23 (shell shape), 24 (ribbing pattern), 29 (mosaicostacum), and 40 (rib flares).

RESULTS AND DISCUSSION

Fifty most parsimonious trees of 208 steps (consistency index = 0.566) were found. The 50% majority-rule consensus tree is presented in figure 1, which can be compared with two previously presented evolutionary scenarios. Kafanov and Popov (1977) produced a phylogram based on two key characters : stomach structure (analyzed by Ya. I. Starobogatov) and Popov's (1977) work on shell microstructure. Kafanov and Popov (1977) considered 38 taxa [only those taxa represented in both my analysis and that of Kafanov and Popov (1977) are shown in figure 2; they considered neither the origin of the Cardiidae nor the group's Mesozoic history]. Only nine of the 28 extant taxa were examined for stomach structure. Starobogatov's study of stomach structure rests heavily on the presence/absence and position of sorting areas, as described by Purchon (1960a). Purchon's (1960a) description of the cardiid stomach came from the study of *Cerastoderma edule* by Graham (1949). Starobogatov (In: Kafanov and Popov, 1977) stated that the SA-3, or posterior sorting area, is absent in *Cerastoderma* based on examination of *C. glaucum* (Bruguère) (Ya. I. Starobogatov, pers. comm.) and *Hypanis*. However, the posterior sorting area (labeled SAP) is the most prominent structure in Graham's (1949) figure of the stomach of *C. edule*. While promoting the utility of using stomach structure to elucidate the higher-level phylogeny of the Bivalvia (Purchon, 1959, 1960a, b), Purchon (1960a:481) warns that "...it is not easy to make an objective analysis of the occurrence and identities of the various sorting areas. The presence or absence, and the degree of development of the various sorting areas has a profound effect on the appearance of the interior of the stomach, and could obscure more fundamental issues such as the course taken by the major typhlosole and the intestinal groove...the occurrence of sorting areas can only be used with the greatest caution for phylogenetic purposes." Although seven of the 20 anatomical characters in the present analysis concern the stomach, none relate to the sorting areas.

Popov's (1977, 1986) classification of bivalve shell microstructure conflicts with those of Carter (1980, 1989), Carter and Clark (1985), Carter and Lutz (1989) and Watabe (1984). The only systemically useful microstructural characters that I have found so far concern the relationship of the ornament to the rest of the shell (characters 28, 29 and 40).

The only cardiid phylogeny suggested by Keen is found in her description of cardiid evolution (Keen, 1980). I have constructed a phylogram (Fig. 3) based on that description.

In the present analysis, *Palaeocardita silberlingi* is located at the base of the cladogram, followed by *Septocardia*, *Protocardia*, and then the rest of the Cardiidae. This topology is in agreement with the ideas of early cardiid evolution suggested by Cox (1949), Keen (1969a, 1980) and Newton (1986). However, the monophyly of *Palaeocardita* is questionable (C. R. Newton, pers. comm.), and the more common species, including the type *P. austriaca* (Hauer) and *P. crenata* (Goldfuss) could be carditoids, whilst *P. silberlingi* is a cardiid. Due to the uncertainty of the taxonomy of *Palaeocardita*, I refrain from placing *P. silberlingi* in a higher taxon within the Cardiidae.

Septocardia was placed in its own family, the Septocardiidae, in the superfamily Tridacnoidea by Kafanov and Starobogatov (In: Kafanov and Popov, 1977). *Septocardia* is clearly a primitive cardiid and it does not share any of the derived features of *Tridacna*. Likewise, *Septocardia* does not belong in the derived subfamily Cardiinae as indicated by Keen (1969a, 1980). *Septocardia* is here placed in the cardiid subfamily Septocardiinae.

The subfamily Protocardiinae has been understood to include the genera *Protocardia*, *Integricardium*, *Jurassicardium*, and *Nemocardium* (Kees, 1969a, 1980). My results indicate that this is a paraphyletic group. *Integricardium* is more closely related to *Lahillia*. The paraphyly of the Protocardiinae has been acknowledged implicitly for some time. McLearn (1933) erected *Onestia* as a subgenus of *Integricardium*; the former was considered a genus by McLearn

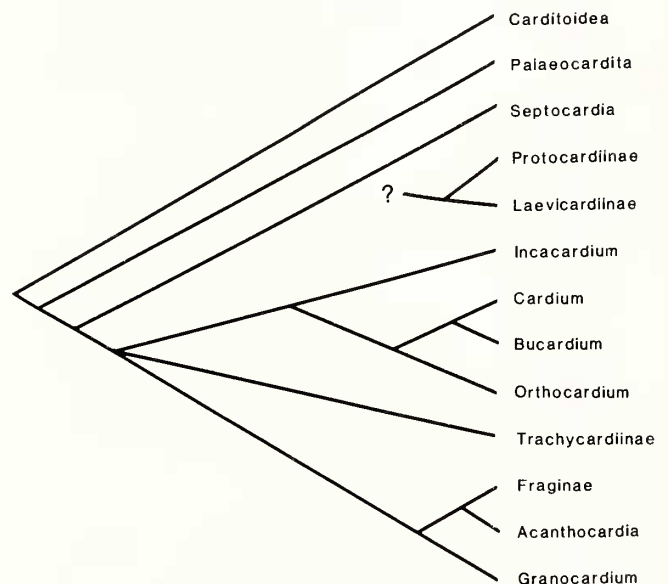


Fig. 3. Evolutionary scenario reconstructed from Keen (1980:24-30).

(1945) and Day (1978), but not by Keen (1969a, 1980). Day (1978) postulated that *Integricardium* is ancestral to *Onestia*, which is in turn ancestral to *Lahillia*. He also placed *Onestia* in the Lahilliidae. Present results indicate that the family Lahilliidae should be relegated to a subfamily (Lahilliinae) within the family Cardiidae (as originally proposed by Finlay and Marwick, 1937), and should include *Integricardium*.

Nemocardium is the sister taxon to the Laevicardiinae. This group is in turn the sister taxon to the rest of the cardiids. Because of its change in ribbing pattern from that similar to *Nemocardium* as a juvenile, to that of *Fulvia* as an adult, *Habecardiium* has been recognized as transitional from the Protocardiinae to the Laevicardiinae (Glibert and van de Poel, 1970; Keen, 1980). Glibert and van de Poel (1970) erected *Habecardiium* as a subgenus of *Laevicardium*, into which some of the species of *Habecardiium* had been placed previously. Keen (1980) placed *Habecardiium* as a subgenus of *Nemocardium*. Popov (1977) and Kafanov and Popov (1977) also placed *Habecardiium* as a subgenus of *Nemocardium*, but did not recognize it as transitional to *Laevicardium* and *Fulvia*, placing the latter two taxa in the Cardiinae. Besides ribbing pattern (24:2), the Laevicardiinae are united by the number of ctenidial pliae (5:2), tentacles that extend only to the bottom of the posterior adductors (10:0), presence of complex eyes (12:1), a centrally located right caecum (18:1), and shape of the cardinal teeth (43:3 and 45:3).

Keen (1969a, 1980) placed all the Cenozoic protocardiines in the genus *Nemocardium*. Other authors (Fischer-Piette, 1977; Popov, 1977; Wilson and Stevenson, 1977; Noda, 1988; Voskuil and Onverwagt, 1989) have raised some of the subgenera to the generic level. It is suspected strongly that the subtraction of *Habecardiium* from *Nemocardium* would leave the latter as a monophyletic group. I decline here to place *Nemocardium* within a subfamily. A systematic analysis which includes all of the subgenera of *Nemocardium* as in Keen (1969a, 1980) represented, plus the Laevicardiinae, is in progress.

Jurassicardium is a monotypic taxon known from only a few specimens. Only the type material is sufficiently well preserved to be of systematic use, and I have not examined it.

The remainder of the Cardiidae comprise those forms typically accepted to constitute the taxa Cardiinae, Trachycardiinae, Fraginae, Clinocardiinae, Lymnocardiidae, and Tridacnidae. Two monophyletic clades can be distinguished within this unnamed taxon. One clade, here considered the subfamily Cardiinae, contains the taxa placed in the Trachycardiinae and most of the taxa placed in the Cardiinae by Keen (1969a, 1980), and all of taxa placed in the Cardiinae (except for *Laevicardium* and *Fulvia*) by Kafanov and Popov (1977). In agreement with Kafanov and Popov (1977), the present results indicate that *Trachycardium* and the related taxa *Acrosterigma* and *Vasaticardium* do not constitute a separate subfamily but are members of the Cardiinae.

The least derived monophyletic group within the Cardiinae contains the taxa *Acanthocardia*, *Rudicardium*, *Sawkinsia*, and *Chrysocardium*. Synapomorphies of this clade are cardiiform shell shape (23:5), tuberculate spines (28:5) and irregular cross-striae (30:1). *Rudicardium* is considered either a subgenus of *Acanthocardia* (Keen, 1969, 1980; Popov, 1977) or a synonym of it (Voskuil and Onverwagt, 1989). These two taxa are united by a suite of hinge characters: incomplete anterior cardinal socket (42:1); shape of the cardinal teeth (43:8 and 45:10); hinge plate overlapping the right posterior lateral socket (48:1).

Cox (1941) erected *Sawkinsia* as a genus of cardiid. Vokes (1953) placed *Sawkinsia* in the Tridacnidae, and was followed by Rosewater (1965), Keen (1969b), and Jung (1976). Stasek (1962) considered the resemblance between *Sawkinsia* and the tridacnid *Hippopus* to be a case of convergence. *Sawkinsia* does not share any of the derived characters of *Tridacna*, nor any of *Tridacna*'s notable autapomorphies: (1) there is no loss of the anterior lateral teeth; (2) the spines are tubercles, not wide and gently curved; (3) nor is there any evidence of the rotation of the shell about the animal. According to the present phylogenetic hypothesis, *Sawkinsia* is a member of the subfamily Cardiinae.

Woodring (1982) erected the genus *Chrysocardium* in the subfamily Fraginae based on a single left valve. *Chrysocardium* shares not only a lunule flap touching the beak (25:3) with *Sawkinsia*, but three characters found nowhere else in the Cardiidae: hinge inversion (36:1) (described for *Sawkinsia* by Cox, 1941); weak myophorous buttress (38:1); double keel (41:1). *Chrysocardium* should be considered a synonym of *Sawkinsia*, however *C. aurum* Woodring, appears to be valid. Except for missing data, the characters for two taxa are scored identically (see appendix 4).

The next monophyletic group includes *Bucardium*, *Cardium*, *Vepriocardium*, and *Dinocardium*, and is united by seven synapomorphies. The close relationship of the first three taxa to each other has been recognized by numerous authors (see Keen, 1969a; Kafanov and Popov, 1977). The position of *Dinocardium*, however, remains uncertain. Keen (1951, 1969a, 1980) placed *Dinocardium* in the Laevicardiinae. Kafanov and Popov (1977), in dismantling the Laevicardiinae, tentatively placed *Dinocardium* in the Cardiinae; Kafanov (1980:298) called the taxonomic position of *Dinocardium* "most mysterious."

The next node within the Cardiinae contains *Austrocardium* and *Cardium acuticostatum*, and is united by lack of lunule flap (25:0) and shape of the anterior cardinal (45:5). Freneix and Grant-Mackie (1978) erected the Cretaceous *Austrocardium* as a monotypic taxon. Wilckens (1904) placed the Cretaceous form *C. acuticostatum* in *Cardium* (*Ringiarcium*) [= *Cardium* (*Bucardium*)], which is otherwise a Miocene to Recent taxon (Keen, 1969a, 1980). The results of my analysis indicate that *C. acuticostatum* belongs in

Austrocardium. There are three other Cretaceous species that differ little from *C. acuticostatum* and *Austrocardium*. These are: (1) *C. denticulatum* Baily, which was placed by Darteville and Freneix (1957) in *Acanthocardia* (*Acanthocardia*); (2) *C. (Bucardium) lillei* Freneix and Grant-Mackie (specimens of which had originally been described as *C. acuticostatum*); (3) *Schedocardia ? waiparana* Freneix and Grant-Mackie. These species should be placed provisionally in *Austrocardium*, as they share the apomorphies of *Austrocardium* but not those of either *Bucardium* or *Acanthocardia*. Except for cases of missing data, the posterior gape of *C. acuticostatum* (33:1) is the only character not scored identically to that of *Austrocardium* (appendix 4). The posterior gape is convergent with that of *Cardium*.

Hedecardium, *Orthocardium*, and *Agnocardia* form a monophyletic clade. *Hedecardium* has been considered variously as a subgenus of *Vepricardium* (Keen, 1969a, 1980), a genus closely related to *Vepricardium* (Popov, 1977), and a genus in the Protocardiinae (Marwick, 1960; Maxwell, 1978). The latter authors derived *Hedecardium* from *Nemocardium* on the basis of its discrepancy in thickness in the ribs across the shell. However, the rib discordance in *Hedecardium* is not comparable to that in *Nemocardium*. In *Hedecardium*, four to six ribs on the posterior slope are split with a furrow running down the middle, and the remaining posterior ribs are reduced in strength (as happens numerous times in the Cardiidae; it was the basis of Keen's [1936] subfamily Laevicardiinae, shown to be polyphyletic). This change from all ribs of equal width to the rib discrepancy seen in *Hedecardium* can be seen in the growth stages of a single shell. Likewise, the early growth stages of *Hedecardium* are circular, and circular shells are unknown in any form of *Nemocardium*. As a juvenile, *Hedecardium* would strongly resemble *Orthocardium*. It is recommended that *Hedecardium* and *Orthocardium* be considered as distinct genera.

Orthocardium has been considered a subgenus of *Vepricardium* (Keen, 1969a) or of *Cardium* (Keen, 1980) or a genus of fragine (Popov, 1977; Kafanov and Popov, 1977). Here, *Orthocardium* is united with *Agnocardia* and *Hedecardium* by concave ribs (32:1), a condition otherwise unknown in the Cardiidae.

The last clade within the Cardiinae comprises *Grano-cardium*, *Trachycardium*, *Acrosterigma*, and *Vasticardium*, and is united by one character, ovate shell shape (23:3). The latter three taxa, united by three synapomorphies, are usually placed in the Trachycardiinae (Keen, 1969a, 1980) or the tribe Trachycardiini (Kafanov and Popov, 1977) within the Cardiinae. Current results support the latter.

The other major clade of cardiids is united by five synapomorphies and generally contains forms that have been assigned to the Clinocardiinae, Lymnocardiidae, Tridacnidae, and Fraginae. Of these the least derived is *Clinocardium*. This taxon was placed in the Laevicardiinae by Keen (1951, 1969a,

1980), but has come to be accepted as the type of the subfamily Clinocardiinae (Kafanov and Popov, 1977; Kafanov, 1980; Voskuil and Onverwagt, 1989). The next node encountered is *Cerastoderma* and *Hypanis*, which is the sister taxon to the *Tridacna* and Fraginae. Synapomorphies of lymnocardiids + *Tridacna* + Fraginae are medium labial palps (1:1), functional byssus in adult (6:2), posterior cardinal socket angle (44:1) and shape of the anterior cardinal (45:9). Yonge's (1936) and Stasek's (1962) suggestion that the ancestry of *Tridacna*'s was close to that of *Cerastoderma* is upheld by the results. Giant clams should be considered as the subfamily Tridacninae within the Cardiidae.

Cerastoderma and *Hypanis* form a monophyletic group. Therefore, as has been argued by eastern European malacologists for some time (Kafanov and Popov, 1977; Popov, 1977; Taktakishvili, 1987; Basch, 1990), the brackish-water forms should be subfamily Lymnocardiinae, and contain *Cerastoderma*. Furthermore, the results support Kafanov and Popov's (1977) contention that the Lymnocardiinae are related closely to the Fraginae.

Five of the seven characters that unite *Tridacna* and the Fraginae are anatomical: tentacle pattern (9:2); large valvule (11:2); centrally located style sac (15:1); presence of a raised bar on the stomach floor (17:1); posteriorly located left caecum (19:0). The Fraginae is united by the presence of ventral appendages on the foot (7:1), absence of a periphonal suture (8:1), and presence of a mosaicostracum (29:1). The least derived taxa, *Plagiocardium* and *Parvicardium*, were placed in the Fraginae by Kafanov and Popov (1977) but in the Cardiinae by Keen (1969a, 1980). *Apiocardia*, *Trigoniocardia*, and *Fragum* are united by eight synapomorphies, all based on hinge characters. Finally, *Trigoniocardia* and *Fragum* are united by six synapomorphies, five of which are anatomical characters: short labial palps (1:0); fewer than ten ridges on the palps (2:1); the inner palp connected to the bottom of the inner demibranch (3:1); fewer than 20 ctenidial plicae (5:0); type 4 gut (13:3); quadrate shell shape (23:2).

From the above discussion it can be concluded that the family Cardiidae includes nine subfamilies: Septocardiinae; Protocardiinae; Lahilliinae; Laevicardiinae; Cardiinae; Clinocardiinae; Tridacninae; Lymnocardiinae; Fraginae. Taxa usually assigned to the Trachycardiinae form a monophyletic group within the Cardiinae. *Dinocardium* is a cardiine closely related to *Cardium* and *Vepricardium*. *Sawkinsia* (= *Chrysocardium*) is transferred from the Tridacninae to the Cardiinae, as it is related closely to *Acanthocardia* and *Rudicardium*.

The Protocardiinae (as presented in the Treatise on Invertebrate Paleontology) is paraphyletic. *Integricardium* is a member of the Lahilliinae. *Nemocardium* is the sister taxon to the Laevicardiinae. The subfamilies Clinocardiinae, Tridacninae, Lymnocardiinae, and Fraginae form a monophyletic group.

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APPENDIX 1.

Classification of taxa used in this study following Kafanov and Popov (1977).
Taxa not listed are not discussed therein.

Superfamily Cardioidea

Family Cardiidae

Subfamily Protocardiinae

Protocardium
Integricardium
Nemocardium
Habecardium

Subfamily Cardiinae

Tribe Cardiini

Cardium

Tribe Vepricardiini

Vepricardium
Agnocardia
Bucardium
Hedecardium

Tribe Trachycardiini

Trachycardium
Acrosterigma
Vasticardium

Tribe Laevicardiini

Fulvia

Tribe Dinocardiini

Dinocardium

Subfamily Clinocardiinae

Tribe Clinocardiini

Clinocardium

Subfamily Fraginae

Tribe Fragini

Trigoniocardia
Apiocardia
Fragum

Tribe Acanthocardiini

Rudicardium
Acanthocardia

Tribe Parvicardiini

Plagiocardium
Parvicardium
Orthocardium

Subfamily Lymnocardiinae

Tribe Cerastodermatini

Cerastoderma

Tribe Hypanini

Hypanis

Superfamily Tridacnoidea

Family Septocardiinae

Septocardia

Family Tridacnidae

Tridacna

Superfamily Arcticoidea

Family Lahillidae

Lahillia

APPENDIX 2.

Classification of taxa used in this study according to Keen (1969a, b; 1980). Taxa not listed are not considered in any of Keen's (1969a, 1969b, 1980) papers.

Superfamily Cardiacea

Family Cardiidae

Subfamily Cardiinae

Septocardia
Granocardium
Vepricardium (*Vepricardium*)
Vepricardium (*Orthocardium*)
Vepricardium (*Hedecardium*)
Cardium (*Cardium*)
Cardium (*Bucardium*)
Acanthocardia (*Acanthocardia*)
Acanthocardia (*Rudicardium*)
Acanthocardia (*Agnocardia*)
Plagiocardium
Parvicardium

Subfamily Trachycardiinae

Trachycardium
Acrosterigma (*Acrosterigma*)
Acrosterigma (*Vasticardium*)

Subfamily Protocardiinae

Protocardia
Integricardium
Nemocardium (*Nemocardium*)
Nemocardium (*Habecardium*)

Subfamily Fraginae

Fragum
Trigoniocardia (*Trigoniocardia*)
Trigoniocardia (*Apiocardia*)

Subfamily Laevicardiinae

Laevicardium (*Fulvia*)
Laevicardium (*Dinocardium*)
Cerastoderma
Clinocardium

Family Lahillidae

Lahillia

Family Lymnocardiidae

Hypanis

Superfamily Tridacnacea

Family Tridacnidae

Tridacna
Sawkinsia

APPENDIX 3.

List of characters and character states.

I. Anatomy

A. Labial palps

1. Length: 0) short, 1) medium, 2) long
2. Number of ridges on palps: 0) ridges absent, 1) <10, 2) 10 - 19, 3) 20 - 29, 4) >29
3. Connection of inner palp with ctenidia: 0) connects behind inner demibranch, 1) connects with bottom of inner demibranch

B. Ctenidia

4. Inner demibranch/outer demibranch relation: 0) Outer demibranch does not overlay inner demibranch, 1) Outer demibranch partially underlain by inner demibranch
5. Number of plicae: 0) <20, 1) 20 - 39, 2) 40 - 59, 3) 60 - 79, 4) 80 - 99, 5) >99

C. Foot

Byssal apparatus: 0) absent in adult, 1) present in adult, but non-functional, 2) functional in adult (see Pelseneer, 1911)

7. Ventral appendages: 0) absent, 1) present

D. Siphons and tentacles

8. Periphonal suture: 0) present, 1) absent (see Pelseneer, 1911)
9. Tentacle pattern: 0) absent, 1) numerous, in both mantle fold and on siphonal area, 2) numerous, in mantle fold only, 3) few, in mantle fold and siphonal area, 4) few on siphonal area only
10. Dorsalmost extension of tentacles: 0) bottom of adductors, 1) to middle of adductors, 2) to top of adductors, 3) beyond top of adductors
11. Valvule (see Pelseneer, 1911) 0) absent, 1) small, 2) large
12. Eyes (see Kishinouye, 1894; Nagel, 1897; Zugmayer, 1904; Weber, 1908; Pelseneer, 1911; Braun, 1954) 0) simple, 1) complex

E. Gut

13. 0) Type 1, 1) Type 2, 2) Type 3, 3) Type 4, 4) Type 5

F. Stomach (see Graham, 1949 and Purchon, 1960a, for general descriptions of bivalve stomachs)

14. T3 (tertiary typhlosole): 0) absent, 1) present
15. Position of style sac: 0) posterior, 1) central
16. T1 (major typhlosole) curved (see Nakazima, 1964): 0) yes, 1) no
17. raised bar: 0) absent, 1) present
18. Position of right caecum: 0) right side of stomach, 1) central
19. Position of left caecum: 0) posterior to right caecum 1) caeca parallel, 2) anterior to right caecum
20. Accessory left caeca: 0) absent, 1) present

II. Shell

A. General

21. Posterior margin: 0) digitate, 1) crenulate, 2) smooth
22. Rib number: 0) absent, 1) less than 70, 2) greater than 70
23. shell shape: 0) carditaform, 1) quadrate - long, 2) quadrate - short, 3) ovate, 4) circular, 5) cardiiform, 6) oval, 7) cerastiform, 8) trigonal, 9) elliptical, 10) oblique
24. Anterior/central rib pattern: 0) concentric, 1) radial, equal in width to posterior ribs, 2) concentric, changing to radial, 3) rib discordance, 4) radial, thinner than posterior ribs, 5) none

Character state tree: (((((5,(7,8)6)4,10,3)2,9)1)0

25. Lunule flap (see Kafanov, 1980, pp. 298-299): 0) absent, 1) raised, does not block beak, 2) blocks beak but does not touch it, 3) touches beak, 4) strongly folded over beak
26. Ridges on lunule flap: 0) absent, 1) present
27. Growth line strength: 0) strong, 1) weak
28. Spines: 0) lumpy nodes, 1) none, 2) round knobs, 3) A-shaped, separate shell layer from ribs, 4) hollow posterodorsally, 5) tubercles, 6) gently curved, 7) hollow keel

Spines are defined as emanating from the top of the ribs. The "spines" of trachycardiines emanate from the side of the ribs, and are considered separately (character 40).

29. Mosaicostracum ("spines" on fragines): 0) none, 1) beads, 2) scales

Mosaicostracum was first described by Hamilton (1969). Keen (1980) and Vokes (1977, 1989) referred to this layer as the intritacalx (D'Attilio and Radwin, 1971). Carter (1989) considers intritacalx synonymous with mosaicostracum. This character is linearly ordered.

30. Cross-striae: 0) simple, 1) irregular, 2) absent
31. Internal rib expression: 0) weak, 1) strong
32. Ribs concave: 0) no, 1) yes
33. Posterior gape: 0) absent, 1) present
34. Dorsal nymph extension, 0) absent, 1) present
35. Posterior umbonal buttress: 0) absent, 1) present
36. Hinge inversion: 0) absent, 1) present
37. Nymph groove: 0) absent, 1) present
38. Myophorous buttress: 0) strong, 1) weak, 2) absent
39. Adductor scar relief: 0) strong, 1) weak
40. Rib flares ("spines" on trachycardiines): 0) absent, 1) strong, 2) weak

This character is linearly ordered.

41. Double keel: 0) absent, 1) present

B. Hinge teeth

- 1) Right cardinal teeth
42. Anterior socket: 0) complete, 1) incomplete
43. Posterior cardinal shape: 1) 1, 2) 2, 3) 3, 4) 4, 5) 5, 6) 6, 7) 7, 8) 8, 9) 9
44. Angle of posterior cardinal socket to horizontal: 0) greater than 40 degrees, 1) equal or less than 40 degrees
45. Shape of anterior cardinal: 0) 0, 1) 1, 2) 2, 3) 3, 4) 4, 5) 5, 6) 6, 7) 7, 8) 8, 9) 9

Rest of hinge

46. Right anterior lateral teeth - ventral tooth continues up into umbo: 0) no, 1) yes
47. Right anterior lateral teeth - ventral tooth inserts into socket: 0) no, 1) yes
48. Right posterior laterals: hinge plate overlaps socket: 0) no, 1) yes
49. Anterior lateral teeth: 0) absent, 1) present
50. Left posterior lateral teeth: 0) weak or absent, 1) strong
51. Nymph overlies posterior cardinals: 0) no, 1) yes
52. Left anterior lateral horizontal: 0) no, 1) yes
53. Left anterior lateral socket: 0) absent or weak, 1) strong
54. Left posterior lateral socket: 0) absent or weak, 1) strong

APPENDIX 5.

Synapomorphies for interior nodes. Nodes numbered as in figure 1. Terminal taxa not diagnosed.

Node	Synapomorphies (Character:State)
1	2:2, 5:1, 9:1, 11:1, 12:1, 14:0, 16:1, 20:0, 43:1
2	23:1, 25:1
3	24:0, 28:1, 30:2, 38:2, 49:1
4	27:1
5	21:2, 22:0, 23:9
6	23:2, 43:2, 45:2
7	24:4, 26:3, 48:1
8	5:2, 10:0, 12:1, 18:1, 24:2, 43:3, 45:3
9	39:1, 42:1
10	1:2, 6:1, 13:2, 19:1, 23:4, 24:1
11	5:4, 10:3, 25:2
12	23:5, 28:5, 30:1
13	25:3, 36:1, 38:1, 41:1
14	42:1, 43:8, 45:10, 48:1
15	21:0
16	18:1, 25:4, 26:1, 31:1, 34:1, 39:1, 42:2, 48:1
17	37:1, 46:1
18	2:3, 5:5, 23:5
19	4:0, 19:2, 50:1
20	25:0, 45:5
21	28:2, 30:0
22	32:1
23	42:1
24	23:3
25	25:1, 28:1, 40:1
26	10:2, 40:2, 43:4, 45:6
27	9:3, 23:6, 42:1, 43:5, 45:4
28	1:1, 6:2, 44:1, 45:9
29	13:4, 23:7
30	9:2, 11:2, 15:1, 17:1, 19:0, 23:8, 30:0
31	7:1, 8:1, 29:1
32	42:0, 43:6, 47:1, 50:2, 51:1, 52:1, 53:1, 54:1
33	1:0, 2:1, 3:1, 5:0, 13:3, 23:2

APPENDIX 6.

Taxa represented by species other than type.

- Palaeocardita*, type species *Palaeocardita austriaca* (Hauer). Species examined: *Palaeocardita silberlingi* Newton *et al.*
- Integricardium*, type species *Integricardium dupinianum* (d'Orbigny). Species examined: *Integricardium globulum* (Whitfield).
- Lahillia*, type species: *Lahillia angulata* (Philippi). Species examined: *Lahillia larseni* (Sharman and Newton).
- Nemocardium*, type species *Nemocardium semiasperum* (Deshayes). Species examined: *Nemocardium beckeii* (Reeve).
- Laevicardium*, type species *Laevicardium oblongum* (Gmelin). Species examined: *Laevicardium laevigatum* (Linne).
- Granocardium*, type species *Granocardium carolinum* (d'Orbigny). Species examined: *Granocardium dumosum* (Conrad).
- Agnocardia*, type species *Agnocardia claibornense* (Aldrich). Species examined: *Agnocardia dissidectum* (Woodring).
- Trigoniocardia*, type species *Trigoniocardia granifera* (Broderip and Sowerby). Species examined: *Trigoniocardia antillarum* (d'Orbigny).
- Tridacna*, type species *Tridacna gigas* (Linnaeus). Species examined: *Tridacna maxima* (Röding).
- Hypanis*, type species *Hypanis plicatum* (Eichwald). Species examined: *Hypanis colorata* (Eichwald).